

- iv. The various species of Bee-eaters, when attacking butterflies, usually choose members of the Papilionidæ and Pieridæ.
- v. The Asilid diptera are formidable enemies to all other living insects. They are, however, present in large numbers only in the northern country, and then only for a limited period of the year.
- vi. In Ceylon a resemblance to the genera *Danais* and *Euploea* is doubtfully of value; in fact, in the neighbourhood of Wood-Swallows it is a distinct danger.
- vii. The mimetic females of *Papilio polytes* are not obviously protected by their mimicry, and as a whole probably suffer about as much, or as little, from the attacks of birds as any other fast-flying butterfly in Ceylon.

40. On the South-African Pseudosuchian *Euparkeria* and Allied Genera. By R. BROOM, M.D., D.Sc., C.M.Z.S.

[Received and Read May 20, 1913.]

(Plates LXXV.-LXXIX.)*

INDEX.	Page
<i>Euparkeria capensis</i> Broom	619
<i>Ornithosuchus woodwardi</i> Newton	624
<i>Ornithosuchus taylori</i> , sp. n.	625
<i>Herpetosuchus granti</i> Newton	626
<i>Browniella africana</i> , gen. et sp. n.	627
<i>Mesosuchus browni</i> Watson	627
<i>Scleromochlus taylori</i> Smith-Woodward	629
Affinities of the Pseudosuchia.....	629

EUPARKERIA CAPENSIS Broom. (Pls. LXXV., LXXVI., LXXVIII., LXXIX. figs. 1-8, 17-20, 22, 24.)

In the collection of Mr. Alfred Brown of Aliwal North are a number of imperfect skeletons of a small Rhynchocephaloid reptile of very great interest, which he discovered in Upper Triassic beds about four years ago. Mr. D. M. S. Watson examined them a year ago, but unfortunately he mistakenly regarded them as belonging to the little acrodont-toothed reptile named by him *Mesosuchus browni*. Though the two forms were met with together and are of about the same size, they certainly belong to different families, if not to different suborders. In a short note communicated to the 'Records of the Albany Museum' (6), I have called attention to the confusion and proposed the name *Euparkeria capensis* for the Thecodont form.

As the type, I take a specimen showing a beautiful skull with most of the skeleton. Though this specimen was in the

* For explanation of the Plates see p. 633.

collection as seen by Watson, it was scarcely at all developed, and he did not recognise that the block of stone contained an almost perfect skull which, had he seen it, would have prevented the confusion of the two animals.

In the type specimen is preserved the skull almost complete but slightly crushed, and with the bones in beautiful condition and showing nearly every detail of structure. A number of cervical and dorsal vertebrae are shown, both coracoids, the interclavicle, the right clavicle and scapula, and the right humerus, radius, and ulna. There are also seen in the specimen the whole of the abdominal ribs in perfect condition, the pelvic bones in good condition, but displaced, and most of the left hind limb. Other specimens show the pelvic bones in position and most of the tail. One specimen shows a dentary with a perfect right pes.

The skull is very similar to that of *Ornithosuchus woodwardi*, and there can be little doubt but that *Euparkeria* belongs to the same suborder and to the same family, though the two genera must be regarded as distinct. From the snout to the occipital condyle the skull measures about 83 mm. From the snout to the front of the orbit is about 45 mm. The orbit is almost round and has an antero-posterior diameter of 23 mm. There is a large antorbital vacuity about 20 mm. in length. The infra-temporal opening measures 18 mm. in height and its greatest antero-posterior length at its lower part is 17 mm. The supra-temporal fenestra is small, measuring 13 mm. by 10 mm. The width across the frontals between the orbits is 14 mm., and the width across the squamosals where they form the temporal arch is 34 mm.

The front part of the premaxilla is missing from the type, but it was probably somewhat similar to that in *Ornithosuchus* and other allied types. It forms the lower half of the posterior margin of the rather large nostril. It supports at least two and most probably three flattened pointed thecodont teeth.

There is no evidence of a septo-maxillary on the face.

The maxilla is a long slender bone, which forms the lower and anterior borders of the antorbital vacuity. The anterior ascending process passes up behind the premaxilla and the descending anterior portion of the nasal, and meets the anterior end of the large lacrymal. The posterior horizontal portion passes back to below the middle of the orbit and meets the jugal. It supports apparently 13 thecodont teeth, of which 5 are preserved in the specimen. These are pointed flattened teeth, very similar in general shape to those of carnivorous Dinosaurs. They are feebly serrated behind and probably also in front.

The nasal is rather peculiar in shape. When viewed from above, it appears as a long narrow bone about twice as wide behind, where it meets the frontal, as in front. In reality the front is as wide as the back part, as it forms a curious downward process behind the nostril to meet the premaxilla. The peculiar shape will best be understood from the figures.

The lacrymal is an unusually large bone. It forms most of the anterior orbital margin. Above, it has a long articulation with the prefrontal, and below, a short one with the jugal. Anteriorly, it has a large development which forms the upper margin of the antorbital vacuity meeting the ascending process of the maxilla. Of the anterior process much is below the level of the general surface of the face, suggestive of the antorbital vacuity having lodged a large gland.

The prefrontal is a small narrow bone which forms about half of the upper orbital margin. It is bounded above by the frontal and nasal and below by the lacrymal.

The frontal is a long narrow bone. Behind, it articulates with the parietal and laterally with the postfrontal, and in front with the nasal and laterally with the prefrontal. It only forms a small part of the orbital margin.

The postfrontal is a small triangular bone which articulates with the frontal, parietal, and postorbital, and forms a small part of the upper orbital margin.

The postorbital is a triradiating bone. The upper process passes upwards behind the postfrontal and meets the parietal. The inferior process passes downwards and articulates with the jugal, partly lying in front of it and forming with it the post-orbital arch. The posterior process is short. It meets the squamosal and forms with it the temporal arch.

The jugal is also a triradiating bone. The anterior process is the strongest. It forms most of the infraorbital arch, forming a long suture with the maxilla and meeting the lacrymal. The upper process meets the postorbital and forms with it the post-orbital arch. The posterior process is long and slender and forms the zygomatic arch meeting the quadrato-jugal.

The quadrato-jugal is an angular bone which supports the quadrate and the jugal and binds them together. Above, it meets the squamosal. A large foramen is present between the quadrato-jugal and the quadrate near the lower part of the bone.

The squamosal is small but fairly strong. It may be regarded as a clasping bone which holds together the quadrate, quadrato-jugal, postorbital, parietal, and opisthotic. A small upper process lies in front of the lateral process of the parietal. The relations to the quadrato-jugal and quadrate will be better understood by the figures given.

The quadrate is a long, well-developed bone. Its upper end is firmly articulated with the squamosal and possibly also with the opisthotic, and also meets the quadrato-jugal. The lower end forms the articulation. There is a large opening between the quadrate and quadrato-jugal. The shape of the bone is seen in the drawings given.

The parietal is smaller than the frontal. It forms the back part of the upper cranial wall and has a postero-lateral process which forms much of the posterior wall of the upper temporal

fossa, and at its outer end meets the squamosal. There is no trace of a pineal foramen.

Behind the parietals and partly wedged between them is a small interparietal. It forms the upper part of the occiput, and partly divides the parietal from the supraoccipital.

The supraoccipital forms the middle part of the occiput. It articulates with the exoccipitals, the interparietal, and the parietals.

The exoccipital forms part of the occipital condyle and passes outwards, fusing with the opisthotic.

Only a small part of the basioccipital shows in the specimen as the middle part of the condyle.

The lower jaw is well preserved. The dentary forms the anterior half, and the angular and surangular the greater part of the posterior half. A large oval opening is seen on the outer side of the jaw between the angular and surangular.

A pair of long rib-like bones represent portions of the hyoid apparatus. These are evidently the ceratobranchials, and indicate that *Euparkeria* had a birdlike tongue.

There are well-developed sclerotic plates in the eye, which are curved as in the bird.

Two slightly displaced bones are probably the proatlas and portion of the atlas. There are probably about 9 or 10 cervical vertebrae, of which the upper 3 or 4 are hidden by matrix. The lower cervicals have comparatively short centra. They are practically amphiplatyan or incipiently procelous. The ribs are double-headed and have small uncinates. There are 2 sacral vertebrae, and apparently 26 presacral. The tail is very long and has powerful chevrons.

The shoulder-girdle is well preserved. There is a long slender interclavicle which is apparently narrow even at its anterior end. The clavicle is also long and slender. The coracoid* is large, measuring 24 mm. in antero-posterior diameter and 16 mm. in its transverse diameter. There is a large oval foramen near the scapular articulation and a little in front of the median plane of the bone. The scapula is long and slender. It measures in greatest length 38 mm., and its lower end is 15 mm. across and the upper end 12 mm. in width. There is no distinct acromion process, and the clavicle has been probably rather loosely attached to the front of the lower third of the bone.

The humerus is very slender. Its length is 36 mm. Only the outer aspect is displayed, and it cannot be seen whether there is an entepicondylar foramen. There is no indication of an ectepicondylar foramen. The deltopectoral ridge is very short.

The radius and ulna are slender straight bones. The radius measures 32 mm. in length and the ulna is probably slightly longer. The manus is lost from the specimen.

* Though to avoid any confusion I have used the universally accepted term "coracoid," as I have elsewhere recently shown the bone ought more properly to be called the "precoracoid."

There is a large broad plastron of abdominal ribs which occupies the whole of the front of the abdomen, from a little behind the coracoid to the front of the pubis. The riblets are all slender and arranged in series of threes—a long outer riblet, a shorter middle one, and a still shorter inner one. In front the innermost series remain free, but on passing back they become ankylosed into united groups of two, three, and four. There are probably four series of riblets to each vertebra. Altogether there are 31 groups of ribs.

The pelvis is preserved in two specimens besides the type, and every detail of its structure is known. The ilium is similar to the type found in *Belodon* and *Erythrosuchus*. The acetabulum is large, and closed, and the ilium has a well-marked supra-acetabular ridge. The iliac crest is developed much more backwards than forwards, and the whole crest measures 28 mm. in length. The pubis is comparatively short and broad. It forms a complete symphysis with its neighbour, and the outer border, which is considerably thickened, passes almost directly downwards. A very remarkable feature of the bone is the presence of two pubic foramina. The upper one, which is apparently the homologue of the normal pubic foramen, is the smaller of the two and is fairly close to the acetabulum. The other is close to the symphysis. In the type specimen both pubes are well preserved and the foramina are exactly similar on both sides. The ischium is a variety of the plate-like form, but long and slender. It has a complete symphysis with the other ischium.

The femur measures in the type 58 mm. : in a second specimen 55 mm. It has a slight double curve as in most reptilian femora. The ends have been largely cartilaginous. On the inner and posterior side, near the union of the upper and middle third, there is a well-marked small trochanter.

The tibia and fibula are not perfectly preserved in any of the specimens, but in one or other both upper and lower parts are shown. They are apparently a little shorter than the femur and considerably more slender.

The tarsus consists of two proximal elements, and probably four distal tarsals. The astragalus is irregularly cubical, and the calcaneum considerably broader than long. There appears to be little in the way of a heel. Of the distal tarsals the 4th is the only large one.

The metatarsals are all well developed, and the 5th has the peculiar Rhynchocephalian development. Of the others the 3rd is the longest. The 4th is slightly longer than the 2nd, and the 2nd considerably longer than the 1st. The 1st, 2nd, and 3rd digits have well-developed claws, but the 4th has the phalanges rather weak and the claw, if present, was very small. The 5th toe also has a small claw, though larger than that of the 4th. The digital formula is 2, 3, 4, 5, 3.

Dermal ossifications are present along the back from the head to at least well down the tail. These are arranged in pairs, one

on each side of each vertebral spine. All the best preserved scutes are about twice as long as broad and have the long axis lying antero-posteriorly.

Some at least of the ribs of the middle region of the body appear to have uncinatè processes. These are little ossifications about 3 or 4 mm. in length and about 1 mm. in width. They are firmly attached to the posterior side of the ribs but not anchylosed. Just possibly, though much less probably, they are small lateral dermal scutes.

Before discussing the affinities of *Euparkeria* and the Pseudosuchians generally, it will be well to consider some points in the structure of the allied genera from Elgin. These very interesting specimens, preserved in the British Museum, reveal a few points in the structure of the group not seen in the specimens of *Euparkeria*, and afford a very thorough knowledge of the suborder. *Aëtosaurus ferratus*, on which the suborder Pseudosuchia was founded, has never been very thoroughly described, but Mr. Watson assures me that there is no doubt that it has two temporal vacuities like those of *Euparkeria* and *Ornithosuchus*, and not one as described and figured by Fraas. Though there is thus little doubt that *Aëtosaurus* belongs to the same suborder, it differs in a good many points from the Elgin and South-African forms.

ORNITHOSUCHUS WOODWARDI Newton. (Pls. LXXVII.-LXXIX., figs. 9, 10, 16, 25.)

The type of this Pseudosuchian is a fairly complete skeleton from Elgin, described in 1894 by Mr. E. T. Newton. The specimen is preserved in the British Museum, and through the kindness of Dr. Smith Woodward I have been enabled to make a fresh study of it in the light of the new knowledge obtained from the allied South-African form. Newton's study of the type has been so thoroughly and carefully done that there is very little in the specimen he has failed to observe, and the points where I incline to differ from him are very few in number. Fortunately the British Museum has recently obtained a second specimen which supplies a number of blanks in our knowledge.

The skull, on the whole, resembles that of *Euparkeria* in all essentials, so far as can be seen, though the cranial sutures are less easily made out in *Ornithosuchus* and the palate is unknown in *Euparkeria*. The skull of *Ornithosuchus woodwardi* is more slenderly built, and it differs in having apparently no interparietal, in the shape of the jugal, in having a much larger antorbital vacuity, and in having the teeth differently arranged. In the restored side view of the skull which I give, and which differs only slightly from that given by Newton, the shape of the various openings and bones can readily be seen. The dental formula of *Ornithosuchus* appears to be i. 3, m. 9 as against i. 3, m. 12 in *Euparkeria*; and there is the further difference that, while in the South African genus only one mandibular tooth overlaps the upper jaw-border, in *Ornithosuchus* there are two

teeth which pass to the outside between the premaxillary and maxillary teeth.

The palate of *Ornithosuchus* is well preserved but not completely displayed in front. The restoration of it which I give is hypothetical only in the prevomerine region and in the basioccipital. The pterygoids are large, as are also the palatines and ectopterygoids, and these three bones of the two sides form a large vaulted bony roof to the mouth. On each side there is a pair of oval openings—one between the palatine, the ectopterygoid, and the pterygoid, and the other between the pterygoid and the palatine. This latter is regarded by Newton as the posterior nares. In this, I think, he is in error. The opening has the borders quite flat, and was probably covered by membrane in life and did not transmit any structure of importance. The pterygoid sends forward a long slender process along the inner side of the palatine which doubtless meets the prevomer as suggested in the figure.

The shoulder-girdle and anterior limb, though lost from the type, are fairly well preserved in the second specimen. The scapula differs from that of *Euparkeria* in being very narrow in the middle and much more expanded at the base. It is much more Dinosaurian in appearance. The coracoid has a rather small foramen, and the posterior border below the glenoid cavity is deeply notched. The interclavicle is narrow and not expanded in front apparently. The clavicles are also slender.

The humerus measures 57.5 mm. in length. There is a well-developed deltopectoral crest, and the general appearance of the bone suggests a comparison with that of the Theropoda. The radius and ulna are not very well preserved. The former measures 47 mm. and the latter 49 mm. Only a few bones of the manus are preserved, and these are apparently displaced. A cast of a specimen obtained by Mr. Watson shows rather more of the manus. There are pretty certainly three well-developed digits, and, I think, evidence of a fourth. The carpus is badly preserved: possibly it was imperfectly ossified.

I have given a restoration of the pelvis for most of which, I think, there is clear evidence in the specimen. The pubis is essentially similar to that of *Euparkeria*, but much more elongated. It has a large single pubic foramen. There is evidently a complete symphysis.

The bones of the hind foot of the type, though much displaced, have been separated out and identified by Newton with marvellous care, and the foot is seen to resemble that of *Euparkeria* pretty closely, the main difference being that the fifth metatarsal shows less of the peculiar Rhynchocephalian development, and the phalanges of this, too, are feebler.

ORNITHOSUCHUS TAYLORI, sp. n. (Pl. LXXVII. fig. 11.)

In 1904, Mr. G. A. Boulenger described some rather badly preserved reptilian remains from Elgin as a large example of *Ornithosuchus woodwardi*. Mr. Taylor, when sending the

specimen to the British Museum, recognised that it was a near ally of *Ornithosuchus woodwardi*, though about $2\frac{1}{2}$ times as large. Mr. Boulenger discusses at some length the question whether the specimen is merely an older example of *O. woodwardi* or a new species, and comes to the conclusion that there are no other differences than those that might be accounted for by difference of age. My comparison of the specimens has led me to conclude that the animals, though allied, are at least distinct species, and I have therefore much pleasure in naming the form after the discoverer.

The specimen shows most of the skull. The jugal is probably perfect but is partly hidden by matrix, and the quadrato-jugal is also nearly perfect. The squamosal and postorbital are much crushed, but the side view of the back half of the skull can be restored with moderate accuracy. Most of the upper side of the skull is preserved, but partly broken and not well displayed. A fairly complete snout with maxilla and premaxilla of what may perhaps be a second individual is also preserved. And as we have the remains of the last maxillary tooth in the first specimen, and the corresponding tooth in the snout-fragment, we can make a fairly complete restoration of the skull. When this is done, the very marked differences between it and the skull of *Ornithosuchus woodwardi* are apparent. The arches are seen to be massive instead of slender bars, and the snout relatively much more powerful. The fact of the two animals being distinct is further confirmed by the fact that the British Museum has recently obtained from Elgin two new specimens—the one exactly corresponding in size to the type of *Ornithosuchus woodwardi*, and the other, so far as can be made out, agreeing in size with the large form. In the new specimen of *O. taylori* part of the palate is preserved, and it agrees essentially with that of *O. woodwardi*. There are two similar openings in the back part, and the pterygoid sends forward a similar but relatively larger anterior process.

HERPETOSUCHUS GRANTI Newton.

This small Pseudosuchian from Elgin is less satisfactorily preserved than *Ornithosuchus woodwardi*, but there is sufficient to show that it is a fairly near ally. The skull differs considerably in its proportions, but probably the essential structure is similar. The palate is narrower, and the anterior process of the pterygoid is relatively broader, and there is only a single opening in the pterygoid region. The shoulder-girdle and anterior limb are differently proportioned, being much more slender, and indicate that the habits of the two genera were different. An interesting point revealed by this specimen is the fact that the manus has five well-developed digits. In the carpus there are at least three elements. The five metacarpals are well preserved, but most of the phalanges are missing.

BROWNIELLA AFRICANA, gen. et sp. n. (Pl. LXXIX. fig. 21.)

In Mr. Brown's collection there are portions of at least two skeletons of an animal rather larger than *Euparkeria capensis* but closely allied to it. The only parts well preserved are the shoulder-girdle, pelvic girdle, and femur. These indicate an animal nearly a half larger than the better known African form.

The following measurements will illustrate the differences in size of the two forms:—

	<i>Euparkeria capensis.</i>	<i>Browniella africana.</i>
	mm.	mm.
Width of base of scapula	15	20
Length of coracoid	24	30
Length of ischium	36	about 50
Length of femur	56	74

In general structure there is a close similarity between the bones, but those of *Browniella* are more massive, and there are numerous minor differences.

The ischium differs in shape in being constricted near its middle, and the pubis, besides being much broader and stouter, differs in having only a single pubic foramen. This difference seems of sufficient importance to justify the placing of this species in a separate genus, and I have much pleasure in naming it after Mr. Alfred Brown, the veteran collector, to whom Science owes such a deep debt.

MESOSUCHUS BROWNI Watson. (Pls. LXXVIII., LXXIX. figs. 12-15, 23.)

Though *Mesosuchus browni* differs considerably from *Euparkeria* and is probably not a Pseudosuchian, it has nevertheless some interesting affinities, and, both from its association with *Euparkeria* and from the fact of the two forms having been confused, it seems well to consider the one along with the other.

As already mentioned, Watson, in his description of *Mesosuchus browni*, had regarded some of the imperfect skeletons associated with it as belonging to the same form. As we now know that most of these skeletons belong to the similar sized but distinctly different *Euparkeria capensis*, it is necessary to redefine *Mesosuchus* to some extent.

The type specimen consists of a badly crushed skull showing the premaxilla and maxilla of the left side in good condition, with most of the lower jaw and most of the palate badly crushed. Much of the rest of the skull is present, but so badly distorted that a restoration is difficult. Of the rest of the skeleton of the type individual almost the whole of the vertebral column from the head to about the middle of the tail is preserved. Of the shoulder-girdle there is practically nothing preserved, though much of the

right arm is seen. The pelvis is badly preserved, but both ischia are well seen and most of the left hind leg.

The premaxilla is particularly interesting in having no inter-nasal process, and in this resembling the bone in *Rhynchosaurus* and *Hyperodapedon*. It has two well-developed acrodont teeth, which are round and blunt. The maxilla is long and narrow, and has 13 irregularly arranged rounded blunt acrodont teeth. A disarticulated quadrate, which is not that of *Euparkeria* and pretty certainly that of *Mesosuchus*, is nearly as broad as long, and much more massive than the quadrate of *Euparkeria*. There are two moderately distinct condyles. Watson's description of the palate cannot at present be added to. "Pterygoid of remarkable shape with a deep posterior ramus applied to the inner side of the quadrate, small external ramus (not well exposed) and long anterior ramus which bears a closely-set series of small pointed teeth. Vomer apparently narrow, with a series of small pointed teeth articulated with anterior end of pterygoid. Other bones of palate not shown. Epipterygoid widened with a deep notch for the optic nerve, touching the top of the deep posterior ramus of the pterygoid. Parasphenoid very large and placed high up in the skull." Most of the postcranial skeleton described by Watson are really bones of *Euparkeria*, while the supposed scapula is really the ischium of *Browniella africana*.

The lower jaw is fairly well preserved in the type specimen. It differs from the jaw of *Euparkeria* in having a relatively small lateral opening and in having the part of the jaw behind the opening larger than the dentary portion. The surangular forms more than the upper half of the outside of the back of the jaw, and the rest is mainly formed by the angular.

The vertebræ are not well preserved. They are of about the same size as those of *Euparkeria capensis*. The cervicals have fairly long spines, and the whole neck is relatively longer than in *Euparkeria*—probably 11 vertebræ may be cervical. Altogether there appear to be, as in *Euparkeria*, 26 pre-sacral vertebræ, and apparently 2 sacral.

The humerus, radius, and ulna are much more massive than in *Euparkeria*, but not very well preserved. The humerus measures 37 mm. in length.

The ilium differs considerably from that of *Euparkeria*, and resembles much more closely that of *Hovesia*. Though imperfectly preserved, the upper part of the ilium is manifestly about twice as deep as in *Euparkeria*. The ischium also differs markedly from that of *Euparkeria* in being relatively much shorter, and having only a short symphysis. The pubes are very badly preserved, but have manifestly been much broader than in *Euparkeria*, though essentially similar in type. The illustrations given show the specimen as preserved and the pelvis restored.

The femur, tibia, and fibula are not unlike those of *Euparkeria*. The femur probably measures 49 mm. in length, and the tibia 47 mm. The tarsus has the bones displaced, but is apparently

better ossified than in *Euparkeria*. There are three large elements and at least two small ones. The rest of the pes is probably of the Rhynchocephalian type.

There seem to have been no dermal ossifications in *Mesosuchus*.

SCLEROMOCHLUS TAYLORI Smith Woodward.

One of the most remarkable of the double-arched reptiles from the Elgin sandstone is the little form named by Dr. Smith Woodward *Scleromochlus taylori*. Though there are preserved in the British Museum the remains of five individuals, and though something is known of most of the skeleton, the animal is too small to be well preserved in the coarse sandstone, and hence our knowledge of the detailed structure is very imperfect. Smith Woodward's description and restoration give practically everything one can be sure about. The skull seems to be essentially similar to that of *Ornithosuchus*.

Affinities of the Pseudosuchia.

Mr. E. T. Newton, in describing *Ornithosuchus* and *Herpetosuchus*, discusses the affinities of the forms. He calls attention to the marked resemblances of the forms to *Aëtosaurus*, and even thinks it possible—as we now know to be the fact—that *Aëtosaurus* has an infratemporal vacuity, and also discusses the relationships with *Stagonolepis* and others of the Parasuchia. A comparison is also made with the Dinosaurs *Compsognathus*, *Anchisaurus*, and others, and with the skull resemblances in the Pterosaurian *Scyphognathus*. In summing up the evidences he says:—"The many points of resemblance between the Parasuchia and certain of the forms usually included among the Dinosauria, have also been noticed by other writers; and the difficulty of separating the two groups is increased by a study of this new Elgin reptile, which holds, as I think, a more intermediate position between the two series than any form hitherto described, for although the characters of its skull and teeth find their nearest counterpart among the Dinosaurs, and the pelvis and limbs might belong to either a Theropodous Dinosaur, or a Parasuchian, the form of the free astragalus is more Crocodilian than Dinosaurian. While acknowledging the difficulty of assigning this new reptile to either of these groups, it seems most in accordance with the facts to place it provisionally with the Dinosaurs."

Mr. G. A. Boulenger, when describing the large specimen of *Ornithosuchus*, criticises Newton's conclusions. He says:—"Much as I admire Mr. Newton's description of *Ornithosuchus* . . . I cannot . . . endorse his conclusions as to the systematic position of the reptile." "Dr. Smith Woodward was nearer the truth when he compared it with *Aëtosaurus*." Boulenger argues that *Ornithosuchus* should be placed with *Belodon*, *Stagonolepis*, and *Aëtosaurus* in the order named by Owen, Thecodontia—a

group which agrees quite as much with the Rhynchocephalia and the Carnivorous Dinosaurs as with the Crocodilians.

Though these two opinions seem at first sight to be at variance they are really pretty similar. Practically, it amounts to this, that in the Pseudosuchia we have a group of primitive reptiles which, while they do not fit into any of the later specialised orders, have affinities with quite a number of other groups.

There cannot, I think, be the slightest doubt that the Pseudosuchia have close affinities with the Dinosaurs, or at least with the Theropoda. This has been recognised by Marsh, v. Huene, and others. In fact there seems to me little doubt that the ancestral Dinosaur was a Pseudosuchian. The skulls of such types as *Euparkeria* or *Ornithosuchus* are practically Dinosaurian even in detail, and the skulls of the early Dinosaurs, such as *Anchisaurus*, differ less from the skulls of Pseudosuchians than those of the early Dinosaurs do from many of the later types. And there is nothing in the post-cranial skeleton that is not just what we should expect to find in the Dinosaur ancestor. The shoulder-girdle is more primitive in retaining clavicles and interclavicle, but these are elements which we know from the history of other groups are very variable and readily lost. The pelvis is almost Dinosaurian, and differs only in having the acetabulum closed. This is an important character; but when we consider the condition in the two nearly allied Monotremes—the one with the acetabulum closed, the other with it open—we see how easily even this character may change. The hind limb is almost Dinosaurian in *Euparkeria*. The ankle is less specialised and the fifth toe is still well developed and retains the Rhynchocephalian characters. *Euparkeria* is in my opinion potentially bipedal, and was probably partly bipedal in its habits. The fourth toe of the hind foot is more feebly developed than the third and the axis of the foot is down the third toe, which would seem to indicate that the feet were at least not so laterally placed as in lizards, and that the animal possibly ran on its hind feet. The relative shortness of the toes also seems to confirm this view, as well as the feebleness of the fore limbs. I believe *Euparkeria* fed on some large forms of insects like locusts, and captured them with its front feet.

Ornithosuchus was probably very similar in habit to *Euparkeria* and was even a little better adapted for running on its hind feet; the large species *O. taylori* could hardly have had the same habits as the small *O. woodwardi*. It is too massively built, and probably had become largely carnivorous, adding to the larger insects various small vertebrates, and perhaps, like the vulture, the flesh of animals too large for it to kill.

The affinities of such small Pseudosuchians as *Euparkeria*, *Ornithosuchus*, and *Aëtosaurus* with the Belodonts through such an intermediate form as *Erythrosuchus* is very manifest. And as Boulenger stated, the Pseudosuchians are about as near to the Parasuchians as to the Dinosaurs. The series of dermal plates down the back, though suggesting affinity is, however, not a

character on which too much weight must be placed. As we see in the Lacertilia, dermal ossifications are subject to great variation in even allied forms.

Another group to which the Pseudosuchians seem to have affinities as suggested by Newton, is the Ornithosauria. In general proportions the Pterodactyles differ very greatly, but the form from which they arose must have been very much like that seen in Pseudosuchians. The Pterodactyl and Pseudosuchian skulls are almost exactly similar in essentials. As pointed out by Newton, the skull in *Scyphognathus* resembles pretty closely that of *Ornithosuchus*. The Pterodactyl manus is simply an ordinary reptilian manus with the 5th digit lost and the 4th greatly specialised, and there can be no doubt that the 5th digit was lost before the wing-membrane was developed. The pelvis of the Pterodactyl is not thoroughly known beyond doubt, but seems to be a modification of the ordinary plate-like type with the prepubis ossified.

Scleromochlus is a very lightly built Pseudosuchian evidently adapted for taking leaps, and not for bipedal progression on the ground. The limbs are long and slender, and the length and slenderness of the fore limb suggest that possibly there was a membrane stretched between the fore and hind limbs and perhaps between the hind limbs and tail, which would enable the little animal to take sustained leaps like *Petaurus*.

Although *Scleromochlus* is already too specialised in the hind foot structure to have been in any way ancestral to the Pterodactyls, it may suggest how they have arisen, just as *Galeopithecus* suggests how the bats arose.

There is still another group to which some Pseudosuchian has probably been ancestral, namely, the Birds. For a time one or other of the Dinosaurs was regarded as near the avian ancestor. The resemblance of the hind limb and pelvis seemed to make this extremely probable, and Huxley, Marsh, Cope, and others have all favoured this view. Others, however, were more impressed by the apparently avian characters in the skeleton of the Pterodactyls, and especially in the striking avian appearances in the brain, and have argued in favour of a close affinity between the Birds and the Pterodactyls. Osborn, while recognising the affinities to both groups, and especially to the Dinosaurs, believed that the Birds and the Dinosaurs had a common ancestor, probably in the Permian. Seven years ago, when describing the skeletogenesis of the Ostrich, I argued that the bird had come from a group immediately ancestral to the Theropodous Dinosaurs. The Pseudosuchia, now that it is better known, proves to be just such a group as is required. In those points where we find the Dinosaur too specialised we see the Pseudosuchian still primitive enough. The bird pelvis has probably developed from a type like that of *Ornithosuchus* by the pubis turning further back and the symphysis becoming lost. Whether the union of the metatarsals is a primary or a secondary character is a debatable point. The question is really whether the bird ancestor was a hopping

bipedal animal before it flew, or if it only hopped after the wing had become specialised. I am strongly of the opinion that it was a hopping animal first, and that the metatarsus became strengthened to support the weight of the body entirely borne by the hind feet. It is easy to understand a hopping animal taking to an arboreal life and ultimately developing a wing out of a four-toed hand, while it seems unlikely that the hind foot could ever have developed by arboreal habits. It is interesting to note that while the ancestor of the Pterodactyls had four toes in the manus, there is very clear evidence from the skeletogenesis of the bird that the latter also had a four-toed ancestor.

A Pseudosuchian which through a bipedal habit had developed a strengthened ankle-joint and a firm metatarsus, and had lost the 5th digit from the manus would meet all the requirements of the avian ancestor.

We know at present too little to discuss the relationship of the Pseudosuchians with *Sphenodon* and with Gnathodonts, nor can we say whether *Hovesia* and *Mesosuchus* should be placed with the Pseudosuchians. There is evidence of a generalised Permian Rhynchocephaloid order which gave rise to the more specialised Triassic groups, but at present we know too few forms and very few even of these are well known, and until our knowledge has much advanced it seems unwise to attempt any further classification. In South Africa we can trace through the Lower Triassic and Upper and Middle Permian beds forms that may be ancestral to the Pseudosuchians, and when these are better known a satisfactory classification will be possible.

I am much indebted to Mr. E. S. C. Dyke for the photographs of *Euparkeria*.

References to Literature.

- (1) E. T. NEWTON.—“Reptiles from the Elgin Sandstone. Description of two New Genera.” *Phil. Trans.* vol. 185, 1894, p. 573.
- (2) G. A. BOULENGER.—“On Reptilian Remains from the Trias of Elgin.” *Phil. Trans.* vol. 196 B, 1903, p. 175.
- (3) A. S. WOODWARD.—“On a new Dinosaurian Reptile (*Sceromochlus taylori*) from the Trias of Lossiemouth, Elgin.” *Q. J. G. S.* vol. lxiii. 1907, p. 140.
- (4) F. V. HUENE.—“Die Dinosaurier der Europäischen Triasformation.” *Geol. u. Pal. Abhand.*, Jena, 1907.
- (5) D. M. S. WATSON.—“*Mesosuchus browni*, gen. et spec. nov.” *Rec. Albany Mus.* vol. ii. pt. iv. p. 296.
- (6) R. BROOM.—“Note on *Mesosuchus browni* Watson, and on a new South-African Triassic Pseudosuchian (*Euparkeria capensis*).” *Rec. Albany Mus.* vol. ii. pt. v. 1913, p. 394.

A full list of other papers will be found in v. Huene's work.

EXPLANATION OF THE PLATES.

Ang. Angular. *B.o.* Basioccipital. *Cl.* Clavicle. *Co.* Coracoid. *D.* Dentale. *Fr.* Frontal. *I.cl.* Interclavicle. *I.P.* Interparietal. *Ju.* Jugal. *L.* Lacrymal. *Ma.* Maxilla. *Na.* Nasal. *Pa.* Parietal. *Pa.o.* Paroccipital. *Pmx.* Premaxilla. *Po.F.* Postfrontal. *Po.O.* Postorbital. *Pr.F.* Prefrontal. *Q.* Quadrate. *Q.J.* Quadrato-jugal. *S.Ang.* Surangular. *Sc.* Scapula. *S.O.* Suprioccipital. *Sq.* Squamosal. *St.* Sternum.

PLATE LXXV.

Euparkeria capensis.

- Fig. 1. Side view of type specimen. $\frac{2}{3}$ nat. size.
 2. Top of skull of type specimen. Nat. size.
 3. Left dentary of a second specimen. Nat. size.
 4. Right hind foot of this second specimen. Nat. size.

PLATE LXXVI.

Euparkeria capensis.

- Fig. 5. Side view of skull. Nat. size.
 6. Upper view of skull.
 7. The quadrate viewed obliquely from behind, showing the relations to the adjoining bones. Small portions of the squamosal and opisthotic are broken off.
 8. Shoulder-girdle, slightly restored and with the probable cartilaginous sternum added in dots. Nat. size.

PLATE LXXVII.

- Fig. 9. Side view of skull of *Ornithosuchus woodwardi*. Nearly nat. size.
 10. Under view of skull of *Ornithosuchus woodwardi*. Nearly nat. size.
 11. Side view of skull of *Ornithosuchus taylora*. About $\frac{2}{3}$ nat. size. Restored from the type specimens.

PLATE LXXVIII.

- Fig. 12. Side view of imperfect skull of *Mesosuchus browni*. Nat. size.
 13. Impression of the teeth of the right maxilla of *Mesosuchus browni*. Nat. size.
 14. Fragment of ilium, and left hind limb of *Mesosuchus browni*. Nat. size.
 15. Fragmentary pelvis of *Mesosuchus browni*. Nat. size.
 16. Shoulder-girdle and fore limb of *Ornithosuchus woodwardi*. About $\frac{1}{2}$ nat. size. Slightly restored.
 17. Top of left ilium of *Euparkeria capensis*. Nat. size.
 18. Acetabular portion of left ilium of *Euparkeria capensis*. Nat. size.
 19. Portions of three lower dorsal ribs of *Euparkeria capensis* showing uncinates. Nat. size.
 20. Right femur, tibia, and fibula of *Euparkeria capensis*. Nat. size.

PLATE LXXIX.

- Fig. 21. Right pubis, left ischium, portions of both ilia and of two dorsal vertebrae of *Browniella africana*. Nat. size.
 22. Right pubis of *Euparkeria capensis*. Nat. size.
 23. Pelvis of *Mesosuchus browni*. Nat. size.
 24. Pelvis of *Euparkeria capensis*. Nat. size.
 25. Pelvis of *Ornithosuchus woodwardi*. About $\frac{1}{2}$ nat. size.
 26. Pelvis of *Gryponyx africanus*. Much reduced.